EVOLUTION AND DISTRIBUTION OF GRASSES

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ABSTRACT

Recent developments in grass taxonomy give a new insight into their classification, and point to a phylogenetic sequence which maps differences in their internal metabolism. Corroboratory fossil evidence is unfortunately exceedingly meager, but it can be supplemented by examining the implications of present-day distributions. The subfamilies are distributed in worldwide climatic belts, but two-thirds of the genera are confined to single continents. Obviously, the genera are poor travellers, so how did the grasses become so widespread? Much depends on the probability of transoceanic transport. The evidence is inconclusive, but it seems likely that the tropical subfamilies spread during the first half of the Tertiary when the maximum water gap was 1200 km. Species distributions are likewise influenced by climatic differentiation and continental isolation. But they sometimes reveal the intervention of other factors, particularly the disruptive effect of climatic change in the Pleistocene. Data from the Afro-montane flora do not support the proposition that species from adjacent, but contrasting, ecological environments are distributed independently. Nor does a mapping of endemics encourage the concept of discrete centers.

CLASSIFICATION

Fundamental to most biological disciplines is the need to identify the organisms they work with, and the primary purpose of taxonomy is to satisfy this need by devising a standardized nomenclature, differential diagnoses and techniques for identification. One of the powerful concepts it has developed for achieving these aims is that of hierarchical classification.

In grasses this classification has traditionally been based upon similarities in spikelet structure. This provides an eminently practical system, but suffers from the defect that spikelets are subject to a good deal of parallel evolution. Yet the method should not be despised, for 80 years ago Stapf (1897) appreciated, on morphological grounds alone, that the Poeae and Eragrostideae were not particularly closely related. Nevertheless, even when parallel evolution was recognized, there was no criterion by which the true kinship could be determined.

The first revolution in classification occurred in the 1930s, when the taxonomic significance of leaf anatomy began to be appreciated. There was shown to be a major division between temperate and tropical tribes, and several subdivisions among the latter. With these findings it was possible to resolve many of the problems posed by parallel evolution, and to propose modifications with some confidence that the system was approaching closer to an expression of natural relationships.

The second revolution started in the 1960s, when it was shown that differences in leaf anatomy could be correlated with differences in photosynthetic pathway. It is now becoming clear that, at the higher levels, our classification maps variations in the internal metabolism of the plants.

Taxonomy, which set out to devise a practical filing system for cataloging plants, has thus acquired a classification which constitutes a source of biological evidence in its own right. To unravel its meaning is inevitably speculative, but

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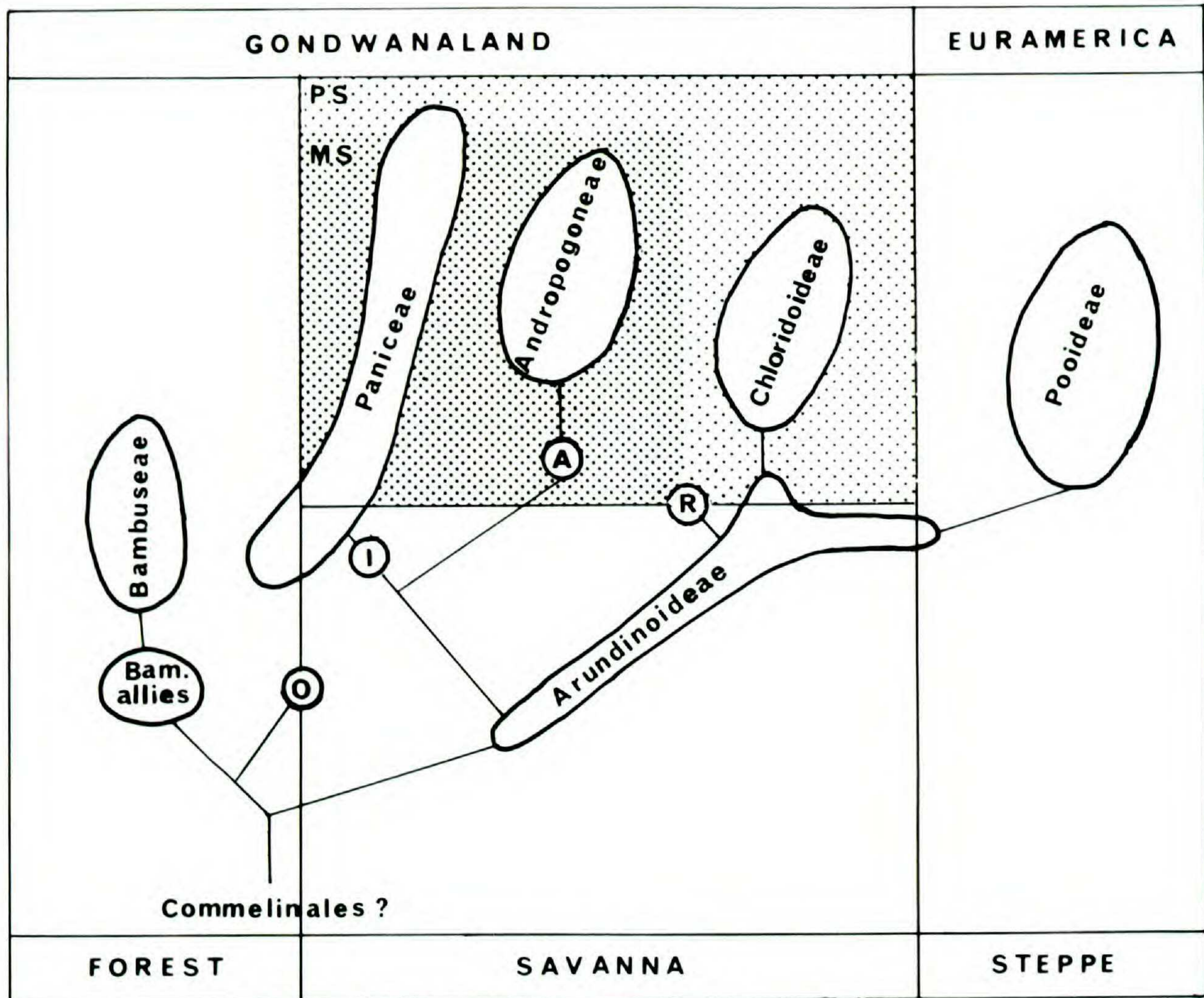[1] Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, Great Britain.

FIGURE 1.   Suggested relationships among the major groups of grasses. A = Arundinelleae, I = Isachneae, O = Oryzeae, R = Aristideae. C_4 metabolism is indicated by stippling; it is divided into the MS and PS types of Brown (1977).

speculation is no bad thing provided we understand it to be no more than a working hypothesis, which gives coherence to a complex web of detail and grants some insight into the probable processes at work.

PHYLOGENY

We know, from the doctrine of evolution, that similarity between organisms is not accidental, but is due, in the first instance, to the chain of inheritance that links them together. We cannot determine this genealogical tree directly, but a good natural classification maps degrees of overall similarity, and should therefore contain sufficient information for us to deduce the main outlines of phylogeny. Let us then look at our classification in this light (Fig. 1).

The origin of the grasses is unknown, but most authorities relate them to the Commelinales in general and the Flagellariaceae in particular; at the very least there seems to be agreement that the most likely relatives are to be found in the tropical forests. Now the Bambusoideae, a subfamily defined by certain anatomical peculiarities such as fusoid and arm cells, is both tropical and primitive. Primitive in the sense that some genera have incomplete suppression of axillary

buds in the inflorescence and spikelets, and the flowers may retain trimerous symmetry. Among them is a group of small tribes (e.g., Olyreae) known as the bamboo allies, which paradoxically combine the primitive and baroque. This collection of curios, apparently the relics of ancient departures from the mainstream of grass evolution, gives some hint of the diversity that must once have existed in the ancestral stock. They are mostly insignificant broad-leaved inhabitants of the rainforest ground layer, which are often mistaken for other forest families such as Zingiberaceae. By contrast their near relatives the true bamboos have become successful competitors in this environment by developing woody tissue and adopting the form of trees. A flaw in this argument is the anemophilous pollen grain of all grasses (Page, 1978), for it seems incompatible with a forest origin. However, Oryzeae is a peripheral tribe of the subfamily, and its predilection for open marshland hints that the primitive habitat might have been glades and margins rather than the forest itself.

However, the future of the grasses lay, not in the forest, but in the tract between forest and desert that we know as savanna. The most likely candidates for the grasses which first moved into this environment belong to the subfamily Arundinoideae, for this is also primitive; primitive in the sense that it lacks distinctive features, but seems rather to represent the lowest common denominator of subsequent subfamilies. Its notoriously difficult taxonomy suggests that it is now reduced to dismembered fragments around a core which has become extinct.

Subfamily Chloridoideae is easy to place for it abuts onto Arundinoideae, and indeed the boundary between the two is difficult to establish. It ushers in a new development, the Kranz syndrome. This is a set of anatomical characters associated with C_4 metabolism, in effect an extra loop in the photosynthetic cycle (the basic form of which is known as C_3), that renders it more efficient in high temperatures (Teeri & Stowe, 1976; Tieszen et al., 1979).

Subfamily Panicoideae presents more problems. It has also evolved the Kranz syndrome, in fact two different versions of it (the MS and PS types of Brown, 1977), but some genera of Paniceae still retain the older non-Kranz anatomy and C_3 metabolism. Moreover, there are no direct links between the main tribes, Paniceae and Andropogoneae. The situation is still rather confused, but a tentative arrangement is shown in Fig. 1.

Finally, subfamily Pooideae seems to represent a new venture for the grasses, an adaptation to cold climates and invasion of the temperate steppes. It has retained the primitive C_3 pathway, for the more advanced form offers no advantage in a cool climate. This suggests a relationship with Arundinoideae, a few of whose genera have shown their ability to penetrate deeply into the temperate zone.

THE TIME SCALE

Phylogeny would be simple if the sequence of events could be dated, but unfortunately the fossil record of grasses is exceedingly meager. However, there are some scraps of evidence relating to three main phases in the development of the grassland ecosystem.

The broad-leaved bamboo allies are a very minor constituent of the forest

ground layer and the woody bamboos themselves are thought to have been a later secondary adaptation. Therefore, whether we regard the closed rainforest as a cradle or museum, the grasses are unlikely to have been of much significance until they established themselves under the lighter canopy of marginal woodland, and assumed something approaching the familiar narrow-leaved life form. We may tentatively associate the onset of this process with the Paleocene, when unambiguous grass pollen first appears in the record (Muller, in litt.). Thereafter the unique potential adaptability of their life form, with its basal tillering, structural combination of stem and sheath, intercalary meristems and substitution of leaf sheaths for the floral envelope, enabled the grasses to move into progressively drier and more open habitats, securing an increasingly important role in the understory of the low interrupted tropical woodland and bushland which presumably occupied this environment. Development of the distinctive savanna physiognomy was aided by fire, for fires started by lightning seem always to have been a feature of the savanna environment (Komarek, 1972); burning is certainly of long standing for the savanna trees have evolved a number of distinctive fire-resistant features. Equally certainly the grass life form is unharmed by fires which destroy many of its competitors. In fact, savanna is an ecosystem in which grass provides the fuel that ensures its own survival.

The second phase of development followed the introduction of herbivores to the system. Contemporary grass-eating mammals have high-crowned teeth resistant to the abrasive properties of the silica bodies in grass leaves, and such teeth first appear among fossil mammals of the Middle Oligocene (Gregory, 1971; Webb, 1977). It can be inferred that grassland had emerged as a vegetation type by this time, and that grasses were undergoing further modifications to mitigate the effect of predation. The mammals responded by reciprocal adaptation, and in doing so they achieved a kind of symbiosis with the grasses, which were able to attract and sustain a level of grazing pressure sufficient to cripple their competitors. The Oligocene also provides the first grass fossils, some spikelets identified as *Stipa* (MacGinitie, 1953), indicating that at last some modern genera were extant by this time.

The third phase was the association of the grasslands with man, who extended and transformed them to support his grazing herds, and to provide the cereal crops upon which he relies so heavily for subsistence. This phase is documented in the archaeological record, but is not germane to the present discussion.

The main point to emerge from the scanty fossil record is that grasses were in existence during the early Tertiary when the continents were in the final stages of separation, and that their history must take this factor into account. The position of the continents at this time has been discussed in detail by Raven & Axelrod (1974) and Raven (1979), but the salient points may be summarized very briefly as follows. Africa and South America were some 800 km apart in the Paleocene, though there were probably intermediate oceanic islands, and moving gradually towards their present separation of 2,500 km. Madagascar-India was already separated from Africa; India parted company with Madagascar in the Paleocene, meeting Asia in the Middle Oligocene. There were probably feasible indirect routs for seed dispersal between Africa, Eurasia, North America and South America during most of the first half of the Tertiary. In addition there was

a direct temperate climate connection between South America, Antarctica and Australia until the Eocene (the connection between South Africa and Antarctica was severed in the late Cretaceous).

Beyond these snippets of fossil evidence, we must make what we can of a kind of fossil that is still available to us, and that is the present-day distribution of grasses.

THE DISTRIBUTION OF SUBFAMILIES

Hartley (1958a, 1958b, 1973) and Hartley & Slater (1960) have produced a series of maps showing the distribution of tribes and subfamilies. Their findings may be briefly summarized as follows:

Paniceae.—Tropical, humid equatorial zone; center in South America.
Andropogoneae.—Tropical, seasonal rainfall zone; centers in India and Southeast Asia.
Chloridoideae.—Tropical, particularly the dry belts of Cancer and Capricorn.
Pooideae.—Temperate, mainly northern but also in South America.

Hartley took his data from a large number of published Floras, calculating the percentage contribution which each group made to the total grass flora. This has the advantage that there is no pressing need to reconcile differences in taxonomic treatments between the various Floras. It yields a useful measure of relative importance, but percentages can sometimes be misleading. Cross (1980) has produced a set of maps using simple species counts, which reveal a number of discrepancies between tribal distribution measured by species abundance, and Hartley's method of relative importance. For example, the Pooideae have a high percentage figure in the north temperate zone where they are undiluted by other groups, but are actually most prolific in the Mediterranean region. She provides additional data on Bambusoideae (tropical) and Arundinoideae (southern subtropical).

From the foregoing it is evident that the major taxa have sorted themselves into worldwide climatic belts. Most of these are more or less sympatric in the tropics, but the Pooideae are radically different, having a predominantly north temperate distribution, and the Arundinoideae display a southern subtropical, possibly relict (Darlington, 1965), pattern. In short there are no surprises, for the distribution of major taxa is entirely consistent with taxonomic prediction.

DISTRIBUTION OF GENERA

To examine this problem the world was divided into 25 areas, and the grass genera scored as present or absent in each. The resulting data matrix was then sorted by cluster analysis (Clayton, 1975).

Disregarding 87 genera whose distribution was essentially worldwide, there were found to be seven clusters of continental extent which together accounted for 450 genera. The remaining 98 genera were shared in various ways between adjacent clusters; some of these genera may have been naturalized introductions (known adventives were excluded from the outset), but well over half were represented by different species in the two parts of their range. They linked the

clusters into two chains: Eurasia, North America, temperate South America; and tropical America, Africa, tropical Asia, Australia.

The two chains are predictable, and strengthen the view that Pooideae are geographically distinct from the rest of the family. However, the discovery that two-thirds of the genera are confined to single continents is disturbing, for it demonstrates that genera are poor travellers, and raises the question of how the subfamilies achieved their worldwide distribution.

The ability of grasses to cross short stretches of sea is not in doubt, but there is no reliable evidence either way on the subject of longer journeys. Transoceanic voyages are certainly very difficult, for most of the wind or water currents have a sufficient north-south component to carry the disseminules into a different climatic zone, and the problem of establishing themselves in the face of native competition is known to be formidable. Moreover the rapidity with which numerous weedy grasses are becoming naturalized in alien territories strongly suggests that these plants, though admirably equipped for dispersal, could not cross the oceans until modern commerce provided a vector.

Of course, the vegetation of oceanic islands testifies that disseminules do arrive by some means or other. However, their flora is usually conspicuously unbalanced by comparison with the mainland, showing clear signs of derivation from a limited number of haphazard immigrants. There is no evidence of this phenomenon if we compare the grass floras of continents. To the contrary, they seem rather broadly based; the major subtribes of Andropogoneae, for example, show much the same pantropical distribution as the tribe itself.

It can also be argued that the low probability of successful transoceanic dispersal may have been offset by the enormous time span available. This proposition can be partially tested, for it implies that the older tribes have the best chance of achieving a wide distribution, and should therefore contain proportionately more of the 87 widespread genera. In fact the reverse is true; the tribes believed to be younger contain a higher proportion of widespread genera. It seems that the distribution of the older tribes is conditioned by their rate of extinction, rather than their rate of dispersal.

The inconsistency between the worldwide distribution of higher taxa, and a demonstrable reluctance of genera to cross the present day oceans, can be resolved by invoking continental drift. It is envisaged that the tropical subfamilies spread across the world during the first half of the Tertiary, the greatest water gap being some 1,200 km across the Atlantic; formidable enough, but nothing like such a strain on plausibility as the present width of the ocean. The older Arundinoids were driven outwards by the greater photosynthetic efficiency, in tropical latitudes, of the newer Kranz subfamilies. In the north temperate zone they gave rise to the Pooideae, and were all but replaced by them, the Pooids subsequently dispersing southwards along mountain chains. In the south temperate zone the Arundinoideae have survived, reaching Australia (together perhaps with some cool tolerant Kranz genera) via Antarctica. During the latter half of the Tertiary genera continued to evolve, but in comparative isolation upon the increasingly separate continents.

It is of interest to note that on the average widespread genera are much larger than single-continent genera, an obvious consequence of the larger area involved.

But they are still significantly larger when calculated on a species per continent basis, an effect presumably related to their greater age. The contrast between large and small genera suggests that two evolutionary strategies may be involved; the surviving, and by implication successful, older genera securely entrenched in their preferred environments which they exploit by complementary speciation, while the younger genera explore new and possibly labile environments by competitive replacement.

DISTRIBUTION OF SPECIES

Species distributions are commonly demonstrated by means of selected examples. Whether the patterns found are applicable to the bulk of the species is left open to conjecture, but there is sufficient of a probabilistic element in plant distributions to cast suspicion on small samples. It is clearly better to work with very large samples, such as the whole of the Gramineae, but this is beset by three main problems.

Firstly, there is the matter of taxonomy, for little faith can be placed in results if the species themselves are in a state of taxonomic or nomenclatural confusion. Fortunately the grasses have attracted more taxonomic attention than any other family of comparable size, and we are now in a position to put together a tolerably accurate catalogue for most of the world except South America. Another facet of this problem is that it is sometimes very difficult to decide whether a species should rightfully be included as a native or not.

The second problem stems from interrelationships between the distributions of species, of habitats and of communities. This is largely a matter of scale, depending on the purpose of the investigation. The present intention is not to examine the ecological sorting of species into communities under the influence of local habitat factors, but to look beyond this to the overall species pools from which these communities are recruited. The sampling unit should therefore be fairly large in order to find the major patterns, while averaging out the finer detail. It has to be assumed that a full spectrum of habitats is repeated within each of these units, a reasonable assumption insofar as the common catenary sequence of soil types is concerned, but not altogether true of unusual habitats.

Thirdly, there are difficulties caused by the large number of species involved, and the often rudimentary nature of available distribution records. The problem becomes more tractable if data collection is inherently simple.

The method adopted was borrowed from ecology, and consisted of scoring each species as present or absent in "quadrats" of country size. The resulting data matrix was first sorted by cluster analysis (a minimum spanning tree), and then refined by inspection. It was satisfying to find that so crude a method actually worked, and that the results were fairly robust even when quite large adjustments were made to the data.

It was found that species are not arranged in a random mosaic, but are superimposed to such an extent that a limited number of generalized patterns suffice to describe their distribution; it seems likely that this is because they have become entrained with the dominant life form of the major vegetation formations. The individual distributions are not coincident but concentric, as might be expected

from the differing degrees of adaptability that exist between species. Consequently the cumulative patterns (phytochoria) have no definite boundaries, but fade away gradually at the edges, and are best mapped by some form of contouring. They also tend to overlap each other to a greater or lesser extent, an effect which may be exaggerated among grasses, which have a great capacity for infiltrating the seral stages of neighboring formations from which competition would otherwise exclude them. Nevertheless, it is important to appreciate that phytochoria do not have mutually exclusive territories in the manner of ecological communities; indeed, the latter are often synthesized from the members of several transgressive floristic elements.

Another feature of species distributions is that two or more subsets may rest within the geographical limits of a wider pattern, thus affording the basis for a heirarchical classification. Three principal categories are usually recognized:

Kingdom. Generally corresponds to the major land masses, and reflects the effect of continental isolation.

Region. Generally corresponds to the major vegetation formations, and reflects the effect of climatic differentiation.

Domain. In many ways the most interesting category, for it often bears little relation to ecological factors, but seems instead to represent a legacy of disequilibrium left by past historic events, notably the disruptive effect of climatic changes during the Pleistocene.

Regional studies have been made by Clayton & Hepper (1974), Clayton & Panigrahi (1974) and Cope (1977). These have subsequently been consolidated in a series of maps showing the distribution of grass species throughout the Old World (Clayton & Cope, 1980a) and in North America (Clayton & Cope, 1980b).

THE AFROMONTANE GRASSES

In working out the distribution of species it has been tacitly assumed that the floras of contrasting, but adjacent, habitats are not distributed independently. This proposition can be tested on data from the African mountains, for it is widely held that the flora of these high islandlike habitats is distributed differently from that of the surrounding lowlands, and constitutes a distinct Afromontane Region. However, when the grasses of the highland Afromontane Region (Clayton, 1976) and lowland Ethiopian Domain (Clayton & Cope, 1980a) are compared, they are found to have much the same geographical extent. There is thus evidence to suggest that the factors determining the present limits of these two floras have been broadly similar, despite the manifest difference in habitats, and that the geographical case for separating them is weak.

Separation of the Afromontane Region has been strongly influenced by the taxonomic affinity of its flora to temperate genera, implying that its original source was quite different from that of the surrounding tropical lowland flora. Presumably its precursors entered from the north. The precursors of the South African montane flora, of similar taxonomic affinity, must have passed along the same route, but the two floras are now represented by quite different species. They have evidently been evolving in situ for a considerable time and their ultimate

origin is not particularly relevant to their present distribution. Although evidence from taxonomic relationships is a valuable aid to understanding the past, it is often associated with an extended time span. We should therefore be wary of accepting it in the same context as the, largely Pleistocene, events which have shaped the boundaries of present-day phytochoria.

ENDEMIC SPECIES

Endemic species have always had a particular fascination for phytogeographers, and they are frequently invoked as a guide to the center of origin of genera of even whole floras. However, when endemics, in the sense of species confined to a single country, are plotted on a map (Clayton & Cope, 1980a), they are found to be surprisingly common. Evidently the notion of a limited number of compact endemic centers cannot be entertained. In fact, endemics are most abundant in the southern tips of continents, where isolation is probably a major factor. But they are also frequent in all the major orogenic zones (the flat pediplain of the Congo-Zambezi watershed is a notable exception), and there is a low background count almost everywhere.

It seems that we are confronted with two contrasting environments. The mountains offer a great variety of niches, and can accommodate a wealth of species; moreover, they are buffered against the worst effects of climatic change, for the vegetation can adjust by shifting its altitudinal zonation upward or downward. On the other hand, the plains offer a relatively uniform environment where evolution proceeds by competitive replacement, and where climatic change entails a major disturbance.

In short, the distribution of endemics gives little support to simplistic interpretations in terms of centers of origin or refugia. Certainly the species-rich mountains may constitute a valuable reservoir of genetic diversity, but it is likely that evolution has proceeded just as rapidly on the plains, though leaving no relicts to mark its course.

CONCLUSION

The history of the grasses is not a simple matter, for it is compounded from the evolutionary thrust of competition, selection pressures exerted by the environment, the degree of isolation imposed by shifting geographical configurations, and disruptive migrations induced by climatic change. Nor is it amenable to a wholly deterministic approach, for many of these factors operate in a probabilistic fashion. Nevertheless, I have tried to show that a coherent story can be pieced together from existing knowledge of taxonomy and distributions. I should emphasize that it is but a working hypothesis, for there are all too many gaps that must, for the moment, be bridged by conjecture rather than fact.

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